Ann. Natal Mus. Vol. 20 (1) Pages 199—216 Pietermaritzburg Dec. 1968

A preliminary study on conchological physio-pathology, with special reference to Pelecypoda

by

P. H. Boshoff

(P.O. Box 4397, Johannesburg)

SYNOPSIS

This study is concerned with pathological and near-pathological functions, and their sequela, which produce certain structural abnormalities in the pelecypod shell. The phenomena are grouped as follows: decremental phenomena of cicatrisation, scirrhosis, atrophy and necrobiosis; hyperplasia; repair processes; tumour formation; pigmentary changes; compensatory balance of valve growth; testaceous distortion of valves; age progressive phenomena. Attention is drawn to the lack of study on the effects of diseases in Pelecypoda, and to the implications which these effects may have for conchological taxonomy.

CONTENTS

INTRODUCTION

Molluscs do not appear to have the same strength of eradicative tissue repulse for invasive faunal, floral and physicochemical pathogens as do warm-blooded animals, probably due to slower marshalling of their poikilothermic defensive processes. A retarded type of defensive reaction does not seem to give rise to phlegmons or locally destructive lesions. Inflammatory lesions can secondarily destroy the host as is encountered in diseases of homoiothermic creatures, for example hyperpyrexia in malaria which kills cerebral tissue; a hepatic abscess may destroy the liver, resulting in metabolic instead of inflammatory termination of life.

This study is an attempt to direct scientific focus on pathological and near-pathological functions where these accompany or precede physiological repair, or on their sequela, which result in certain marks or lesions on the bivalve shell. A lesion resulting from disease might be taken, albeit mistakenly, as a species characteristic or variation. Hence

some taxonomic errors may creep in. That conchological aberrations can occur under deviate ecological conditions, is known (Cooke, 1959:69-90). Appearances such as dwarfing, stunting, thinning, and thickening have been referred to, and attributed to thermal variations, lime deficiency, extent of ambient water volume and salinity changes (Cooke op.cit.).

The observations recorded below were made during general field studies on Pelecypoda, and are without laboratory or experimental corroboration. Etiological explanations are therefore semi-conjectural. Nevertheless, they may serve as a pointer to taxonomists who may be unaware of such pitfalls, and future ventures into the field of invertebrate pathology may be stimulated.

In taxonomy the term "variety" is frequently applied to a form which presents itself often enough in a reasonably large series of specimens, it having developed in a fairly uniform and favourable environment. Conventional habitats may be sited geographically far apart, yet the characteristics of geoecomorphs under inspection from such separated regions should remain reasonably comparable. Away from this "normal" habitat the occasional variations occuring among specimens should be suspected of having a pathological or near-pathological affliction. The term should be restricted to anamorphs of genetic origin. It may be less strictly employed when scientific accuracy of description is not required. Non-genetic variations may appear where long-standing ecological factors enter into the picture and where signs of pathogenicity are obscure. A taxonomist must attempt to establish and isolate physio-pathological cases. Variant forms might occur so regularly in a certain kind of habitat that they may come to be regarded as a norm. If, however, the isomorph can be re-bred in a subsequent generation from aberrant stock (by repatriating the aberrants from "abnormal" to "normal" ecological surroundings), then the aberrant or "variant" is not of genetic origin and evidence of possible pathology should be recognizable. True bridging forms should be phenotypically different but genotypically identical. Both physiologically and pathologically altered forms are uncritically called ecomorphs, polymorphs or geoecomorphs, thereby failing to distinguish between eco-

Plate I.

Fig. 1. *Spondylus hystrix* Röding. A growth cessation line near margin of shell. Hyperplastic in appearance. Valve on the right in the photograph shows varix formation (arrows). Small perforating holes from algal invasion. Interior of shell shows green patches—algal pigmentation. Spatulate clubbing of spines, particularly those infested by algae, were produced at the growth stage when the mantle edge was producing the sculpture. Spec. in coll. of Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.

Fig. 2. *Periploma fractura* Boshoff. Arrows indicate where air bubbles can be seen through the fragile valves. At umbo a short fracture line is evident, extending at right angles to end at the boundary of the nepionic cap.

Fig. 3. *Periploma fractura.* Broken-off piece of the umbonal region shows a natural fracture at right angles to the hinge border, the left vertical edge on the photograph. Specimens lodged in S. Afr. Mus., Cape Town. Locality: 29°29'S./31° 45'E.

Fig. 4. *Cardium flavum* Linn. Outline ventrally flattened with valve slightly in-curled where the edge has closelypacked decremental concentric lines caused by an attempt to generate continuation of growth. Had such regrowth been successful, this region would have possessed a rather thick concentric varix. Spec. in Natal Mus., Pietermaritzburg. Locality: Inhaca Isl.

Fig. 5. *Divaricella dalliana* Vanatta, showing commencement of its characteristic smooth streak from the umbones to the first growth rest line. Immediately peripheral to the first and second pronounced growth rest lines, the elbows of the divaricate lines (. & ..) are reinstated, albeit somewhat crippled in arch outline, and again become obsolete on further normal growth. Spec. in coll. of Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.


1
2
3
4
5

logical and genetical factors. Under such names the existence of possible pathological agency also has no place. In systematic conchology one finds ecomorphs caused by eco-pathology being described as distinct species. Hence there is a necessity for the collective study of adequate series, as well as the scrutiny of available ecological information, before a decision is made on any taxonomic designation for a shell.

Pathological conditions produced by parasites (Fischer, 1950) will not be considered. Conchological physio-pathology deals with effects seen in one organ of the animal, the shell. The shell will show its specialised pathology relative to the general pathology of the mollusc. A shell is avascular, reparable only in certain parts (inner layers and the margins) and it reflects the lesions of a neighbouring organ, the mantle.

The physio-pathological entities hitherto observed can be listed as follows:

1. DECREMENTAL PHENOMENA: CICATRISATION, SCIRRHOSIS, ATROPHY AND NECROBIOSIS.

At this stage of conchological pathology these are difficult to separate and are often inadvertently used as general terms. Scirrhosis may well encompass the phenomena of atrophy, cicatrisation and necrobiosis. It will here be used as descriptive term applied to the "naked eye" appearance of abnormal testaceous tissue. A growth-cessation concentric line on a shell is not true atrophy or necrobiosis but is an almost normal process, often periodic in some bivalves, e.g. *Phacoides peritaphros* Barnard (1964:479) which leaves a visible "scar." In many Gastropoda and Pelecypoda the growth-cessation line is a regularly and normally occurring mark but in some shells (*Murex*) it is prominent, heralded by a preceding varix (Tryon, 1882:20). Besides normally occurring growth cessation lines from seasonal variations, lack of food also causes growth lines which may border on pathological lesions. In a growth-rest line the deposition of shelly material is of minimized extent and volume, thus leaving a concentric sculptural alteration. Grosser cessation lines (appearing as scirrhotic tissue) suggest a longer stoppage of growth or, at least, its retarded progression over a more extended time period. Such prolongation of pathological influences indicate tabescent influences, which cause a wizened growth zone by deposition of modified tissues. Atrophy is a process of wasting away of already formed tissues. Necrobiosis is the phenomenon where a portion of a living organ dies and becomes replaced by secondary tissues. Neither of these two processes can be applied to testaceous material in any precise way. Decremental lesions are responsible for the testaceous tissue exhibiting catamorphosis, a dequalitate condition with an appearance different from the accepted normal (See Pl. I,

Plate II

Fig. 1. *Spondylus hystrix* Röding, marginal portion. Same shell as in Pl. I, fig. 1. Arrows indicate hyperplastic varices. The peripheral part has regenerated the shell's characteristic sculpture except for one spike which tends to be spatulate as a result of detritus deposition.

Fig. 2. Same as fig. 1. Disturbed sculpture posteriorly. The secondary and tertiary radial riblets, instead of being nodose or finely spinose, tend to be squamate while the sharp spines on the main radials are thickend and broadened.

Fig. 3. *Petricola bicolor* Sow. Posterior part showing disappearance of radial and sub-cancellate sculpture, and their replacement by a closely packed series of scirrhose lines. In its upper littoral habitat this specimen was subjected to periods of desiccation and to fresh water insult. Spec. in coll. of Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.

Fig. 4. Interior of same shell as in Pl. I, fig. 4. Shows edge thickening and straightening of ventral outline by tiered layers of decremental testaceous material.

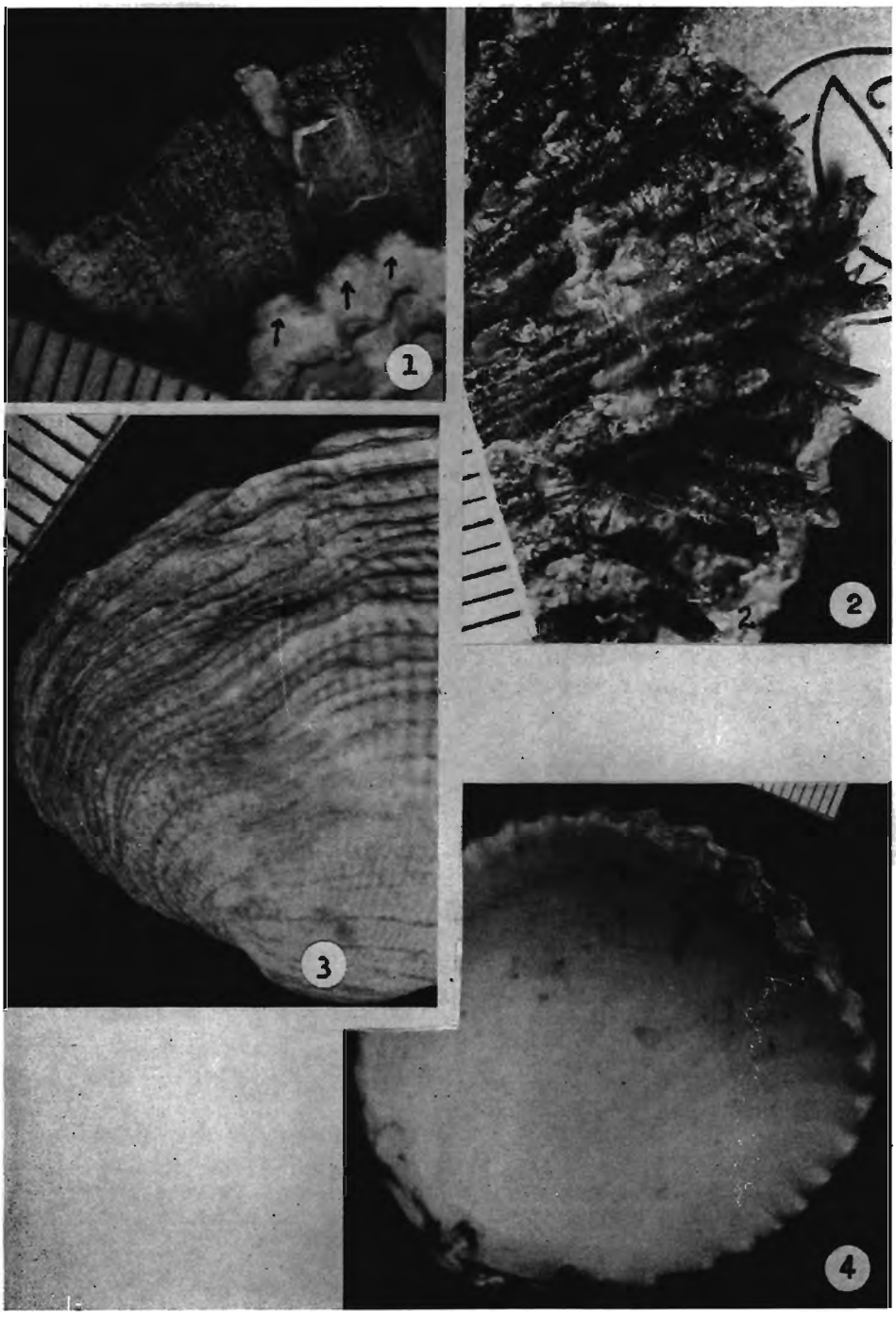

1
2
3
4

fig. 1; Pl. II, figs. 1, 2, 3; P.l III, fig. 1; Pl. V, fig. 4; Pl. VI, figs. 4, 5, 6.). The valve's shape is altered thereby and its sculpture warped.

Decremental lesions, analogous to the atrophic and necrobiotic scars of soft tissue, are usually caused in molluscs by more severe disorders than the almost physiological states of undernourishment and of seasonal "hibernation." It is for future histological study to reveal what kind of tissue alteration is present in scirrhotic testaceous zones. Pathological scarring and deliquescence therefore tend to alter both the outline of a shell (Pl. I, fig. 4; Pl. II, figs. 3, 4; Pl. III, figs. 1, 2; P.l IV, fig. 4; Pl. V, figs. 3. 4; Pl. VI, figs. 4, 5,) its convexity (in *Septifer bilocularis* (Linn.), *Divaricella dalliana* Van.; see also Pl. II, fig. 3; Pl. III, figs. 1, 2; Pl. IV, fig. 4; Pl. VI, fig. 4) and often its sculpture (in *Chama gryphoides* Linn.; see also Pl. I, fig. 1; Pl. II, figs. 1, 2, 3; Pl. IV, fig. 2). *Leda gemmulata* (Sow.), Pl. IV, fig. 3, increases its number of dorsal radial riblets[4], because of decremental processes.

It is commonly observed that where a concentric zone of scirrhosis is present on a bivalve, the adjoining peripheral resumption of healthy growth invariably re-establishes the original and typical sculptural characters of the shell (Pl. II, fig. 1; Pl. V,fig. 2). It may also return to sculpture typical of its juvenile stages, e.g. *Divaricella* (Pl. I, fig. 5). On a pathologically disturbed valve the characteristic sculptural pattern is to be sought immediately peripheral to the scirrhotic zone.

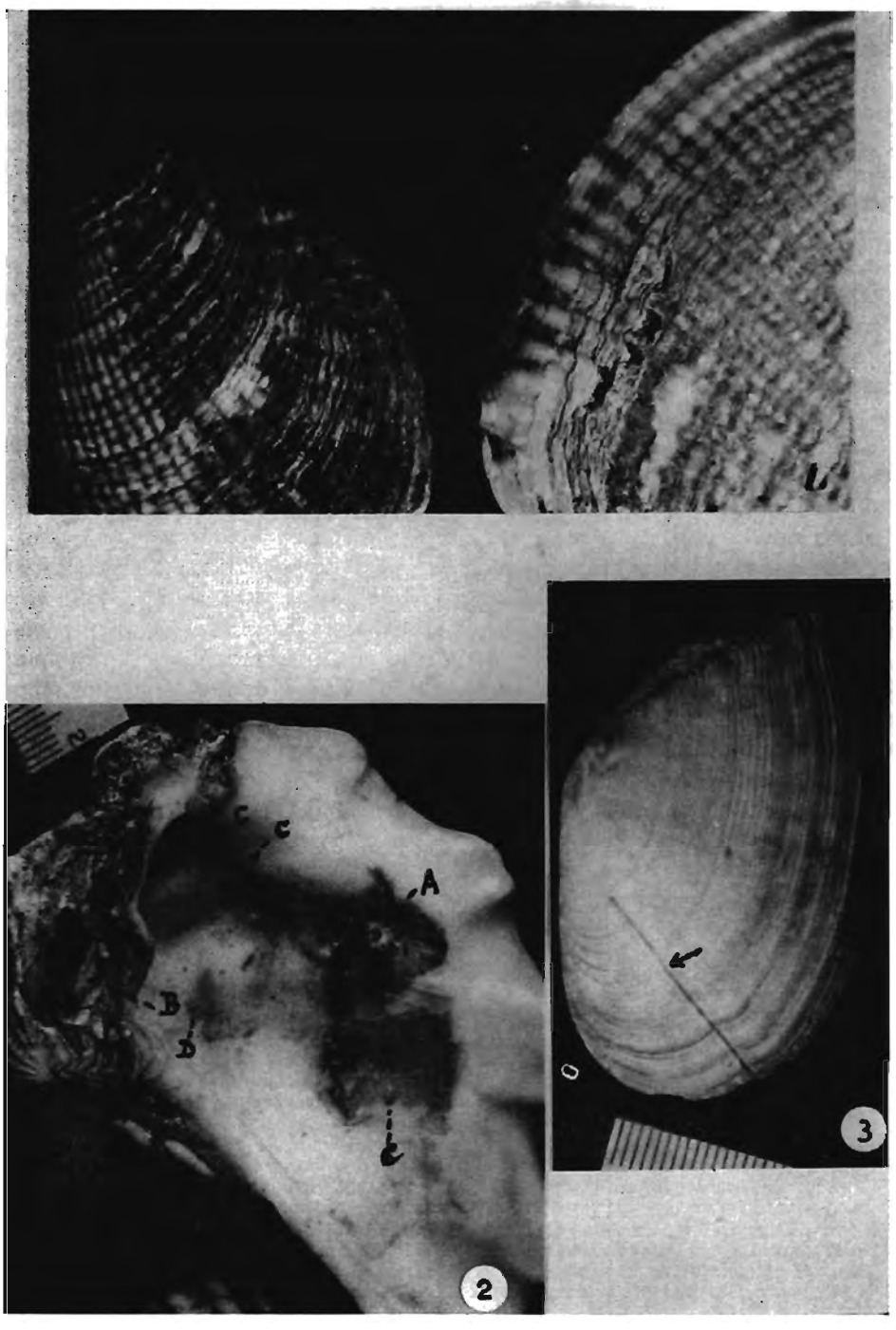
Physiological atrophy occurs as a normal phase in a shell's development, e.g. the median hinge teeth of the *Navicula* and the *Barbatia* groups of Arcidae become obsolescent (Iredale, 1939), or the hinge denticles in *Pinctada capensis* (Sow.) disappear (Barnard, 1964:413), as an age progressive phenomenon. A point of permanent damage on the mantle's edge produces a persistent radial furrow (Pl. III, fig. 3; Pl. V, fig. 3; Pl. VI, fig. 3).

Plate III

Fig. 1. *Gafrarium divaricatum* (Gmelin). Posterior regions of two specimens. On the left, serial decremental lines concommitant with inhibition of posteriad expansion, giving rise to a short form. On the right the specimen shows similar lines of scirrhosis with inroads at four places made by a more destructive process causing such loss of shelly tissue—bryozoan colonies were lodged here at time of collection (primary or secondary?). Lodged in coll. of Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.

Fig. 2. *Tridacna maxima* Röding. Exhibits posterior abbreviation with hinge pathology (borer at *B* not responsible). Its epiconchal juvenile portion conforms to the average shape of *T. maxima* although it is smooth from probable abrasive erosion. Due to some pathogenic process this mollusc underwent necrobiosis to the extent of losing its total hinge region. It regenerated this region by interior nacreous re-layering underneath the slough of the juvenile part, relining the pedal opening and also forming a secondary atypical hinge. This restoration of valve growth at the level of the internal layers gave rise to a misshapen resilium with slight amphidetic positioning; unsymmetrical testaceous lining of pedal lips as well. At the time, in this subvital specimen, invading algae caused green monticules on the inner aspect (as at *D*). Borers also invaded, a large one lodged in the crevice between the juvenile slough and the new hinge, penetrating along the firm matrix of the resilium (as at *B*). Over the lateral aspect of the valve several *Lithophaga* penetrated into the nacreous layer with only initial perforation and, presumably finding that the borable matrix had come to an end, they stopped their movements. This timely cessation of boring explains the absence of nacreous reaction and also suggests the absence of an acidic irritant. *A*, marks the site where a borer is just about to migrate into the adductor muscle and at *C* several small borers had penetrated the nacre in a similar manner. Spec. in Natal mus., Pietermaritzburg. Locality: Inhaca Isl.

Fig. 3. *Tellina virgata* Linn. A mantle lesion occurred at a point antero-ventrally, immediately beyond the early adult region. This left a permanent spot of inactivity on the mantle edge. A well-marked sulcus (arrow) marks its effect throughout the rest of the shell's growth. The sulcus is bounded by centripetal incurving of the concentrics. Internally it is underlain by a hyperplastic nacreous ridge. Spec. in Natal mus., Pietermaritzburg. Locality: Inhaca Isl.


A
B
B
C
C
2
3

2. HYPERPLASIA

Hypertrophy means enlargement or overgrowth of existing tissue constituents, while hyperplasia indicates additional formation of similar tissues, shelly tissue being under present consideration. Hyperplasia is also applied to the overgrowth of certain elements of a tissue only. In the absence of histological studies, the term is here confined to macroscopic appearances.

Hyperplasia occurs commonly. It can be seen as the thickening of older pinnate shells, especially where these are subject to irritative abrasion. When the mantle is stimulated (irritated) by an abrasive agency (? vibration, indentation when worn thin, shock wave production, direct excoriation), it will respond by production of additional shelly material. Hyperplastic change in the sculpture of *Spondylus hystrix* Röding results in spatulate, even foliate expansion of the usually spinose tips, while the basic linear sculpture inbetween the spikes and costae remains unchanged (Pl. I, fig. I; Pl. II, figs. 1, 2; vida infra). It appears in *Spondylus* under conditions of detrital deposition on its shell; and similarly, in *Chama gryphoides* Linn. and *Chama ratoi* Boshoff (1967a: spec. no. 72. It may be that *Malleus anatinus* (Gmel.), with its thickened valves, is a hyperplased senile form of *Malleus regula* (Forsk.) (Boshoff, 1967a: spec. No. 36). In how far hyperplasia is an adaptive characteristic of the older examples of *Pycnodonta hyotis* (Linn.) is an interesting speculation. The spongy tissue of its thickened valves in older examples, is often filled with filamentous algal or poriferan ramifications suggesting super-imposed invasive pathology. The valvular consolidation of *Pinctada margaretifera* (Linn.) as an ageing process, is physiological but suggests pathological agencies when such thickening is premature. In instances of premature hyperplasia one can usually detect the influence of detritus deposition, abrasion or of restriction of movement in narrow confines. Hyperplastic over-repair can be of mantle or of periostracal origin, the former along the valve margins and internal surfaces, and the latter only during the period when the pathogen is sited at the valve edge. The tensillium may possess fibrous regenerative properties as is suggested in the instance of *Periploma fractura* Boshoff (Pl. I, figs. 2, 3). A varix (loosely employed) is a patch or ridge of hyperplastic, maybe hypertrophic, tissue. In some instances, processes of repair are of hypertrophic and|or hyperplastic character.

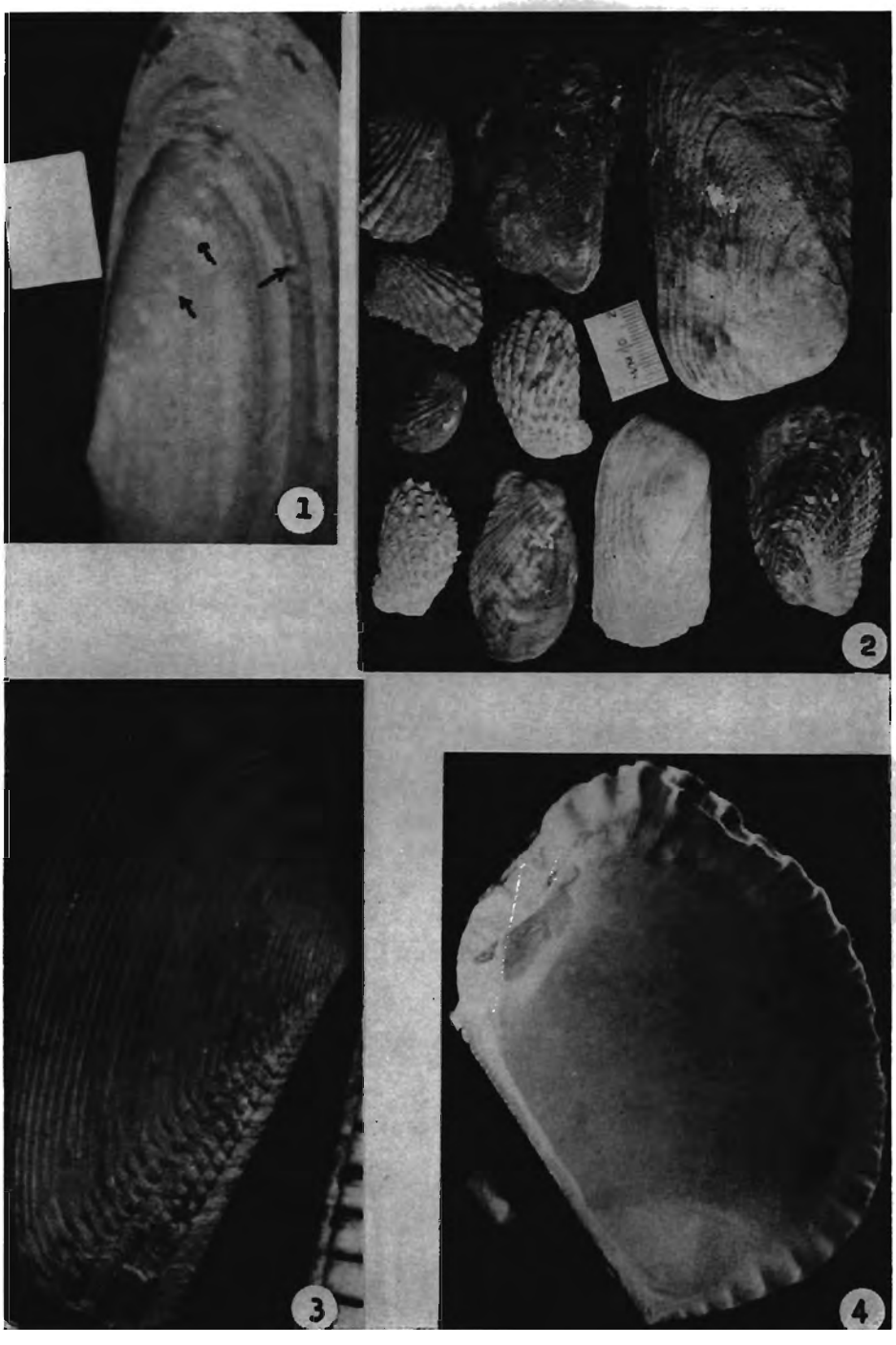
Plate IV

Fig. 1. *Lutraria oblonga* Chemnitz. Posteriorly are areas of deliquescence from probable chemical disturbance while in the mud of its habitat, Durban Bay. Pits (arrows) suggest loss of calcium either by dissolution or by acidic action. Spec. in Natal mus., Pietermaritzburg. Locality: Durban Bay.

Fig. 2. *Cardita variegata* Brug. A group of representatives of this species. Bridging forms are available but were not included in photograph. Two of these specimens actually resemble *Trapezium* sp. superficially. Note the pinholes made by invaders (? poriferan; ? algal) and also the calcified layer of gypsinian growth on the posterior part of the largest specimen (arrows). In coll. of Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.

Fig. 3. *Leda gemmulata* Sow. This five-ribbed "variant" (normally four-ribbed) in all examples seen, starts with a scirrhotic pathology soon after the juvenile stage, lengthwise splitting the second radial costa and forming scabrae instead of nodules along its length. Scirrhotic compaction is particularly well seen near the posterior end. Spec. in S. Afr. mus., Cape Town. Locality: 29°30'S./31°28'E.

Fig. 4. *Arca antiquata* Gray, var *hankeyana* Rve. At posteroventral corner and along posterior border, pathology inhibited the expansion to normal shape. Attempt at growth resumption by a new internal layer of nacreous material. Had further growth been successful, it would have left a large varicose concentric externally. Occurs commonly, but this particular specimen has been lost. Locality was Inhaca Isl.


1
2
3
4

3. REPAIR PROCESSES

These are basic in living tissue, but overrepair and absence of repair border on the abnormal. Repair along the mantle edge or by the visceral mantle on the inside aspect of the valve is seen in Pl. II, fig. 4; Pl. III, fig. 2; Pl. IV, fig. 4; Pl. V, figs. 1, 3; Pl. VI. figs. 1, 2, 5, 6. The material of repair may, occasionally, be of fibrous nature. A naturally occuring fibrous repair presents itself in *Periploma fractura* (Boshoff, 1968). The tissue of repair in this *Periploma* is continuous with that of the hinge tensilium from where it is suspected to originate. In these extremely delicate valves the force of muscular adduction (conversely, the strength of resiliar rebound) consistently fractures the nepionic portion of each valve at right angles to the hinge line, immediately anterior to the beaks (Pl. I, figs. 2, 3.). The pliable fibrous repair gives an ability to absorb future valve strain, thus preventing re-fracture. There is, therefore, fibrous as well as testaceous repair to be found in bivalves. Extraneous external repair by calcium deposition can occur as a fortuitous over-lay by parasitic or symbiotic calcogenic biosis.

4. TUMOUR FORMATION

This results from mantle products forming on a shell's edge or internal layers; some valves produce nacre, others the usual shelly material. If these tumours are of accepted shape and quality, they are called pearls. When *Lithophaga* drills into the shelly matrix of a bivalve to reach the deep layers, one observes an almost total absence of defensive barrier reaction. When such a boring mytilid penetrates through to reach the interior of a shell, it suspends its drilling operations as soon as it finds that there is no more firm matrix to drill into. This desistence obviates the necessity for its victim to counteract with testaceous defence walls (Pl. III, fig. 2). Poikilothermic tardiness partly accounts for the absence of any reaction by the mantle at the time of lithophagal penetration and for lack of any anticipatory signs of resistance. When algae or sponges penetrate to the level of the internal shelly layers, a timely defensive reaction takes place, resulting in the deposition of "walling

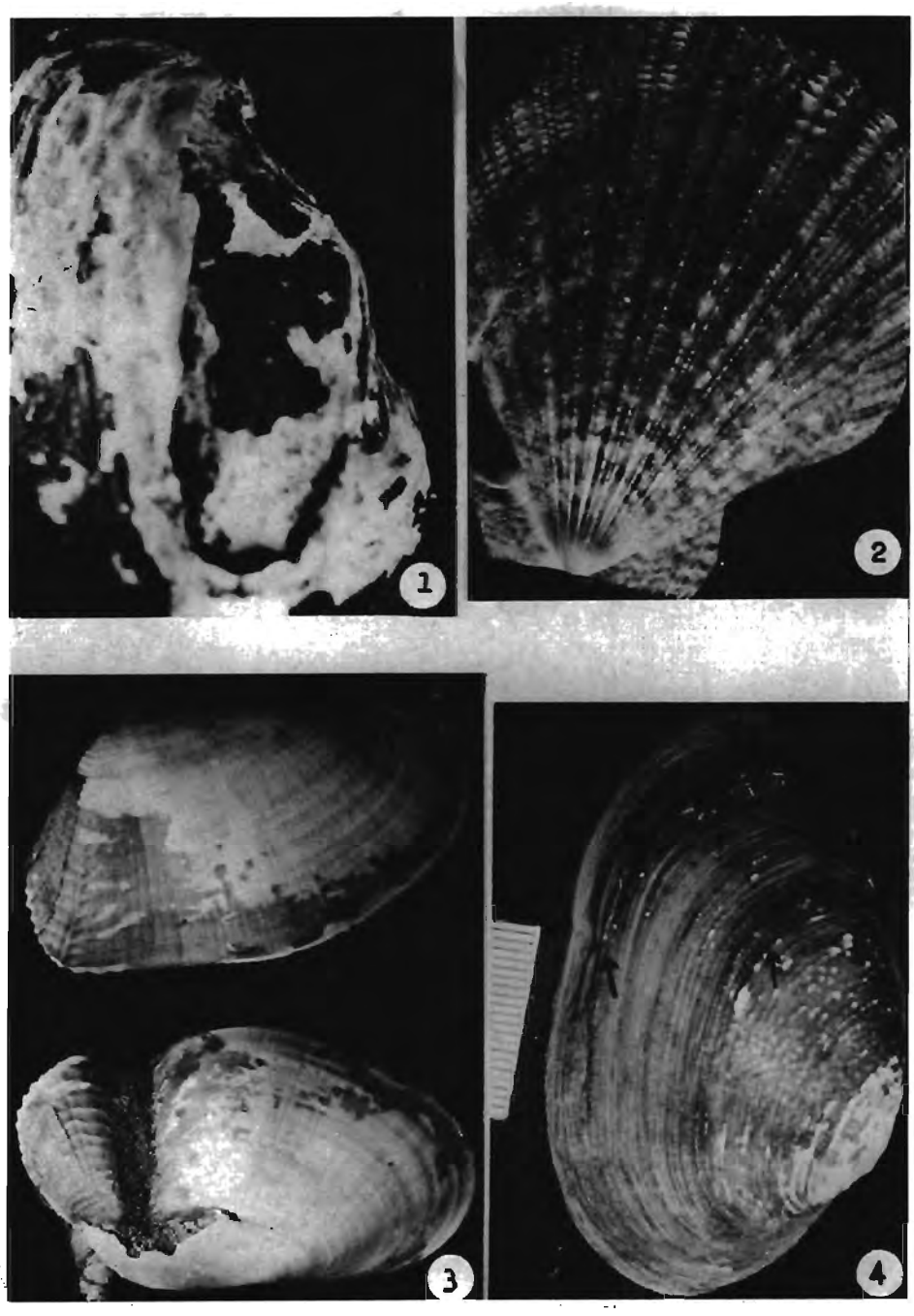
Plate V

Fig. 1. *Aspatharia wahlbergi* (Bernardi). Originally, the juvenile must have been denuded of its periostracum and the shell thereafter worn thin, erasing the umbones. Dissolution of its calcium aided the thinning of erosion. An inner layer of re-deposited nacre reinforced the area internally and marginally re-established progression of growth peripheralwards, leaving an undermined furrow around the originally thinned portion. The re-instituted growth contains shallow pits which could have resulted from further chemical insult in its habitat (mud). In Natal mus., Pietermaritzburg. Lomati river, Hectorspruit.

Fig. 2. *Chlamys senatorius* (Gmel.). Note presence of concentric pathological growth line 9 mm. from shell margin (arrow). Peripheral to this the border zone of the valve shows a luxuriant re-establishment of sculptural features. Close to the pathological linear lesion (near arrow) is a shallow depression where sculptural details remain disturbed and replaced by wizened tissue as a result of the persistence or non-recovery of the mantle deficiency. Spec. in Natal mus., Pietermaritzburg. Locality: Inhaca Isl.

Fig. 3. *Donax serra* Bolten. Juvenile edge of right valve (lower one in photograph) acquired an edge fracture with under-edge intrusion of foreign matter between it and the mantle. This was underscaled by new growth from the inner shelly layers, but the mantle damage remained, as evidenced by the deep, broad, radial furrow and marginal notch on ventral border. The left, healthy valve adjusted its shape to conform with that of its afflicted partner. Spec. in Natal mus., Pietermaritzburg. Locality: Muizenberg, C.P.

Fig. 4. *Cafferia connollyi* Pilsbry. Its mud-living habits exposed it to corrosive agents. Arrows indicate shrivelled concentrics. Spec. in Natal mus., Pietermaritzburg. Locality: Alicedale, C.P.


1
2
3
4

off" nacre. Here, the preceding chemical or physical irritants probably stimulate an apparently early counteraction.

Mantle response to irritation is the stimulus for tumour formation. Mantle response can occur when it underlies a thinned portion of a valve so that deposition of matrix can give reinforcement. Is it possible that the stimulus in this instance could be vibration, indentation or transmitted impacts? It is not uncommon to observe (in *Arca* and *Tridanca* spp.) that the tumor is of greenish colour on the internal aspect of the shell when the sive agent happens to be of algal origin.

5. PIGMENTARY CHANGES

Slightly reduced daylight penetration produces enrichment of colours, for example when a shell lies in water of medium shallowness, 0.3 - 3 m. datum depth. In shallower water than this, the porphyrin pigment of the shell is bleached by the sun, e.g. *Circe scripta* (Linn.). Benthic specimens also are pale, having no actinic stimulation to promote pigmentation. The chlorophyll-like tint after algal invasion on the inner aspect of shells of some species of *Arca*, *Tridacna*, *Ostrea*, and other genera, or on their tumours, is a pigment inclusion of pathological origin. The blackening of Ostreidae when they grow under sand, is attributed to under-oxygenation (Korringa, 1956). Lack of pigment, or its increase, may be present in scirrhotic zones on a valve.

6. COMPENSATORY BALANCE OF VALVE GROWTH

Accompanying a fracture repair, or after a catamorphic process on one of the valves of a lamellibranch, one would expect to find an obviously inequivalvular state to exist. However, the unaffected partner valve seems to have a compensatory mechanism of growth adjustment, contorting to fit the shape of the deformed opposite member (Pl. V, fig. 3; Pl. IV, fig. 4). This mechanism may be brought about by a neural reflex to control symmetry. Pathological doming of a right or a left valve may be present, yet the margins of the unaffected partner valve will still approximate, not necessarily by secondary doming.

Plate VI

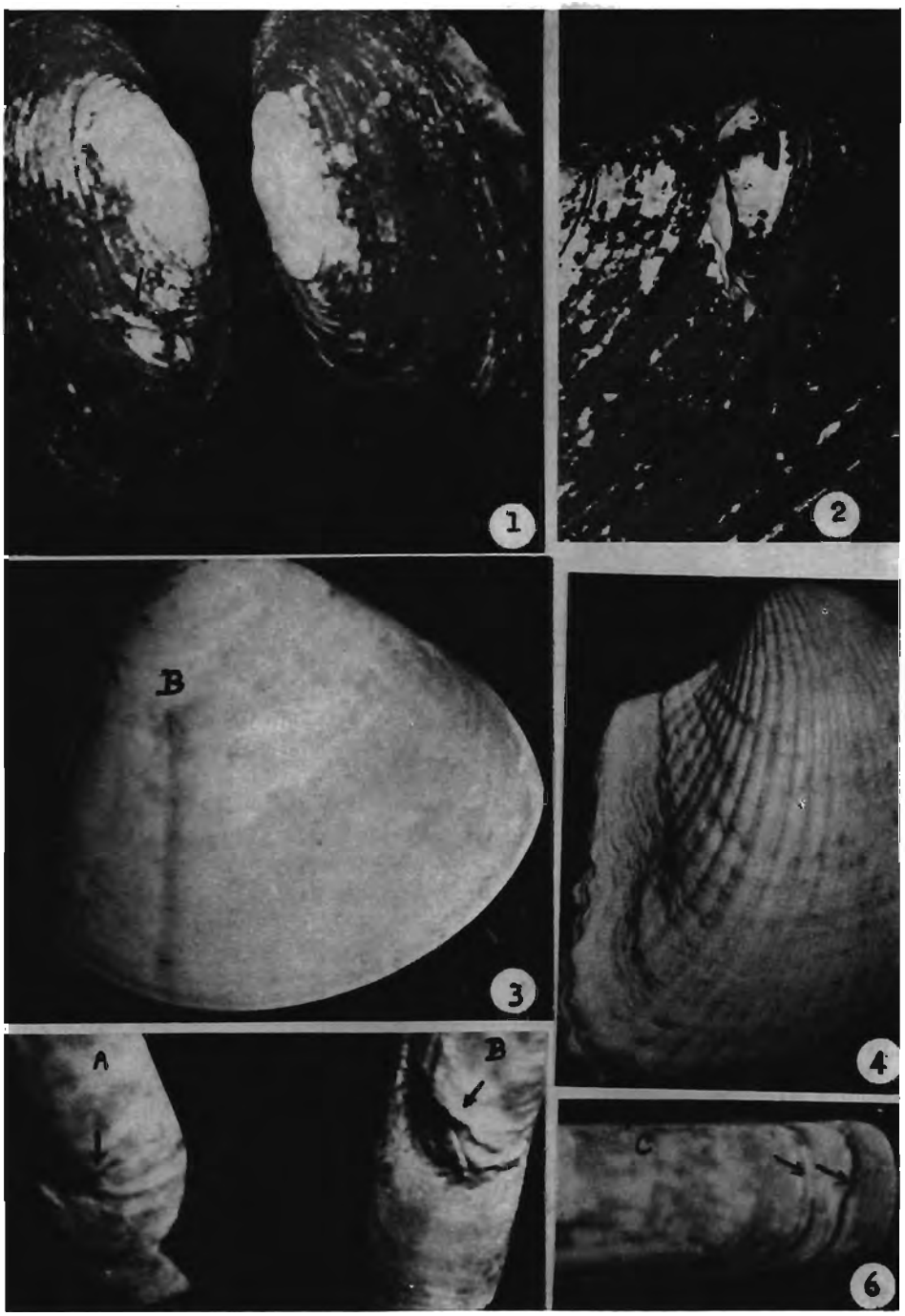
Fig. 1. *Aspatharia wahlbergi* (Bernardi). Arrow points to subelliptical fractured flake on left valve, 11 x 23 mm., slightly depressed. Repair by internal nacreous relayering. R. valve shows a compensatory growth pause, even forming a shoulder without any signs of pathology present—a purely localised retardation. The juvenile portion has a totally denuded periostracum.

Fig. 2. Same as fig. 1. Close-up view of depressed fracture. Spec. in Natal mus., Pietermaritzburg. Locality: Matlabas river, N. Tvl.

Fig. 3. *Venus* (*Meretrix*) *meretrix* Linn. Significant scarring at *A* with peripheral continuation of decremental material causing a radial furrow. At *B* a similar lesion from also a permanently damaged part of the mantle edge leading to persistence of a radially directed scar. In Natal mus., Pietermaritzburg. Locality: Inhaca Isl.

Fig. 4. *Arca antiquata* Gray, var. *hankeyana* Rve. Posterior part of R. valve has an almost squamate overlapping type of diseased concentric. Due to persistent mantle edge insufficiency, there is a retardation of growth giving an outline almost like *Arca natalensis* Krss., but not having any of its other characteristic features. Spec. in Natal mus., Pietermaritzburg. Locality: Inhaca Isl.

Figs. 5 & 6: *Solen roseomaculatus* Pilsbry. At *A*, a crack across the elongate valve stimulated underlapping nacreous repair (arrow) resulting in normal continuance of growth. At *B* the growth response beyond the site of repair is still of the scirrhotic type. Fig. 6. at *C* shows periostracal hyperplasia, being a fibrous repair of a lesion. Shells in Natal mus., Pietermaritzburg. Locality: Inhaca Isl.


1
2
B
3
4
A
B
C
6

7. TESTACEOUS DISTORTION OF VALVES

This can occur from ecological factors, such as desiccation and space restriction. The commonly occurring example of both conditions is demonstrated by *Crassostrea cucullata* (Born). It is well-known that they acquire various shapes when crowded or lodged in narrow spaces. Certain eco-morph forms of *Crassostrea* are often relegated to a separate species when they possess spinose gutters on the upper valve, caused by desiccation. On transplanting a rock covered by a supra-littoral spinose crassostreal colony to a depth of constant immersion, these animals change their form and appearance, and lose their guttered spines (not necessarily shape, depending on space dictates) within the period of one year (Boshoff, 1967c). Transplanted the opposite way, it takes almost double the times before 50% of them assume the forma *spinosa*. Specimens of *Crassostrea* from infra-littoral depths conform mostly to formae *plicata*, *mytiloides* and *cornucopiae;* in the mid-littoral zone formae *frons* and *pestigris;* while in the supralittoral zone, washed by spring tides only, assume the formae *vitrefacta* and *spinosa*. Under conditions of desiccation the upper valve either acquires additional layers of calcification (forma *vitrefacta*) or the edges of the prismatic layer curls up to form gutter-like and tabular projections (forma *spinosa*).

8. AGE PROGRESSIVE PHENOMENA

These are physiological and are well recognized by the conchologist. They still often escape attention, particularly where the adult's appearance does not resemble that of the juvenile, e.g. *Divaricella dalliana* Van., *Venus verrucosa* Linn., *Petricola bicolor* Sow. Barnard (1964) in his monograph on South African lamellibranchs relegated many such a designation by W. H. Turton to *species delenda.*

Zoodynamic processes of repair and formation of defence barriers lead to shape, size, weight, colour and sculptural variations to the confusion of the taxonomist. The environmental agencies responsible for these can be many and varied. Hereunder are listed some of the agencies which fall under suspicion:

(*a*) **Abrasion** can result from water friction, wavelets, particulate matter suspended in water currents, the rubbing of the valves and the neighbouring structures against one another, and by wear from the shell's own mobility. The abrasive erosion of matrix from the posterior margin of shallow water Pinnidae reshapes the curved portion of *Pinna bicolor* Gmel. to assume the squarely truncate shape of *Pinna muricata* Linn. Similarly, with the passing of time, *Atrina squamifera* Sow. often loses its rows of surface bracts. *Crassostrea cucullata* (Born) when subjected to heat abetted by wave onslaught (alternate desiccation and soaking) resists erosion by thickening to assume the forma *vitrefacta.* Wave action seems to affect the shape of *Arca obliquata* Gray so that the lagoon-inhabiting forms show attenuation of shape when compared to those derived from wave-beaten shores (Boshoff, 1967a, spec. No. 17). When *Tridacna* is embedded in coral talus its scales may become worn down so that finally only wavy concentrics remain, or it may become quite smooth as is commonly seen on the boring *Tridacna, T. crocea* Lam. On South African *Lithophaga* viz. *L. obesa* (Phil.), *L. mucronata* (Phil.), *L. nasuta* (Phil.), *L. barnardi* Boshoff (1967a: spec. Nos. 26-29), there are generally one or two small areas of denuded periostracum present, probably from their mobile contact with burrow walls. Contrary

to the opinion of Deshayes (in Tryon, 1882:55) that this mytilid uses an acid as a help in moulding its burrows, none of these bared patches show signs of chemical etching, and support appears to be given to the concepts of Hancock and Agassiz [10B] that the burrows are formed by mantle or by ciliary movement. Confinement in and abrasion against the surrounding rock of its crevice shelter gives rise to "polymorphism" in *Arca helblingii* Brug. and *Cardita variegata* Brug. (Pl. VII and Pl. IV, fig. 2 respectively). The correct terms for this should be paramorphism. The external sculptural features in *A. helblingii* are similar to those of *Arca erythraeoensis* Jonas and it is not impossible that the two may be conspecific, the latter being a sand-living ecomorph of *A. helblingii* (Boshoff, 1967 spec. Nos. 10, 11.). Where abrasion by sand is not too destructive, thin shells protect themselves by thickening their valves, as can be seen in *Pinctada*, *Atrina* and *Pycnodonta*.

The wear and tear resulting from mobility in the case of swimming bivalves such as *Pecten*, show as abrasion evident along the hinge area (beaks disappear) and as the spoiling of sculpture over the surface of the left valve (the lower one when it lands after a leap). Any eroded patch on a shell's periostracum affords foothold for symbiotic and parasitic growths like calcifying algae, Foraminifera, sponges and bryozoan species.

(*b*) **Deposition of silt and detritus** smothers the tissues under their coverage. The resultant exaggerated efforts by the mantle to shift the covering deposit, gives rise to nacreo-deposition of unusual shapes. Such effects can be studied in *Spondylus hystrix* Röding

Plate VII

Arca helblingii Brug. Various shapes demonstrating paramorphism in this shell. The shell, second from the top left and the one below it, show denudation of sculpture from rubbing against its crevice confines. The large specimen on the right top shows no such abrasion owing to its being a fixed valve, as evidenced by the adherence of a portion of coral, *Porites solida*, near its umbo. The shell below it shows a well-retained periostracum. Spec. in Inst. Invest. cient. Moçamb., Lourenço Marques. Locality: Inhaca Isl.

where its fine spiniform processes on the main radials thicken, become spatulate (Pl. I, fig. 1; Pl. II, figs. 1, 2.) and later foliate. The confusingly different sculptural appearances assumed by Chamidae, varying from smooth external surfaces, through squamate to frilled appendages, result from deposition of detritus and leptopel, particularly on specimens living in susceptible positions on the sea-bed.

(*c*) **Actinic effects.** It has already been mentioned that strong sunrays cause bleaching in the majority of species. Conversely, those shells found in the dark, under rocks particularly, e.g. *Malleus regula* Forsk., *Isognomon perna* (Linn.), can be pale and of milky transparency (Tryon, 1882:25).

(*d*) **Temperature changes.** Structural variation, such as excessive formation of growth rings in sub-littoral shells, seems to be caused more by the rise and fall of temperature than by its uniformity at a higher or a lower centigrade level. Abnormal thickness of valves and stunting of growth have been attributed to this agency (Cooke, 1959:84). Also, melanism occuring in shells along the West coast of America is said to result from temperature changes (Cooke, op. cit.). Unless the temperature variations kill the mollusc or reduces its resistence to invading pathogens, it can well be imagined that such a climatic swing can result in a temporary retardation of growth causing a growth rest concentric.

(*e*) **Effects of crevice confines.** Intermittent pressure by the shell against the walls of confined spaces, re-shapes a nestler as it grows, to fit its restrictive shelter. This occurs among nestlers while borers remain unaffected, the latter being able to drill their burrows to a suitable size. *Arca helblingii* Brug. exhibits paramorphism (Boshoff, 1967a: spec. No. 12) as a result of its nestling habits (Pl. VII.). As a member of this species grows older, some of its hinge teeth become obsolescent, either in the lateral or median group as the shape of the shell may demand. In closely confined specimens of *A. helblingii*, the sculpture on the valves' convexity is often abraded. Valves of *Malleus regula* (Forsk.) become restricted as to space solely because of crowded conditions while in byssal attachment to *Cymodocea* stems, and accordingly they assume all kinds of body curvatures and shapes. On examples living in isolation the "polymorphism" is not traceable to any ecological factors. *Isognomon perna* (Linn.) similarly exhibits "polymorphism" whether or not in confined spaces under rock or coral debris. The development of *Streptopinna saccata* (Linn.) when submerged in solid coral matrix (usually in *Porites solida* Forsk. or *Goniopora savigni* Dana) gives rise to an attenuated shape and symphonotic closure of the ventral gap, while leaving a wider than usual edge-indurated posterior opening situated flush with the surface of the coral head in which it happens to be lodged.

The bivalves, *Cardita variegata* Brug., *Septifer bilocularis* (Linn.), *Crassostrea cucullata* (Born), among others, are often subdivided into subspecies (Boshoff, 1967a: spec. Nos. 30, 59, 62). more so when the series under examination was not numerous enough for bridging phenotype variants to be included or when ecological data had been neglected by the collector. Each such "variant" can appear to be so divergent from its sibling that their identity as a single species only becomes possible when the bridging forms are available. When a monomyaric shell exhibits " polymorphism" the adductor muscle has to change its position of attachment in order to exercise a more adequate control over valve apposition. In some such specimens an additional resilifer notch originates along a hinge line which

normally exhibits only one chondrophore (*Pinctada capensis* Sow.) (Boshoff, 1967a: spec. No. 34)

(*f*) **Desiccation.** This agency is responsible for the curling up of the prismatic layer in *Crassostrea cucullata* (Born), forma *spinosa*, and also for the compensational thickening of the upper valve in the same species, forma *vitrefacta* (Boshoff, 1967a: spec. No. 59). These have been discussed under testaceous distortion (section 7, supra).

(*g*) **Physiological and Chemical agencies.** Some genera (*Lithophaga*) bear external deposits of calcium as a normal feature on the periostracum. It is suspected that the features and form of these deposits are determined by the presence of fine periostracal hairs which become obscured by incorporation in the calcified mass. The deposit is so constant in appearance and so reliable a feature that it is of importance taxonomically, for example to differentiate between the *Diberus* and *Leiosolenus* subgenera. Some kinds of calcified deposits, for example on *Ostrea cristagalli* (Linn.), are not of physico-chemical origin but of algal construction. Parasitic and symbiotic attachment of epizootic and epiphytic colonies on to a valve, appears mostly on the anchored species of bivalves. Those lamellibranchs which are well endowed with a periostracum rarely acquire symbiotic, parasitic or other invasive elements on the exterior unless there is a dehiscent or damaged part of the periostracum.

Hunger is a physiological condition which causes a retardation or temporary cessation of growth. The mark of growth cessation is usually linear in the absence of any additional pathology, otherwise a broader zone results. Where the growth line is broader than usual, it will possess a decremental tissue structure owing to pathogenic factors concommitant with the condition of famine, for example, superimposed nutritional oedema of the mantle edge. Invasion by unknown pathogens (possibly physical, such as sand) along the side of the siphon retractors, leave their defacing imprints along the floor of the pallial sinus in one or both valves.

Lowered salinity of sea-water exercises deleterious effects on some marine bivalves if they are not of species accustomed to such variations. Fresh water affects a mollusc when it lives in the intertidal zone where it may be subjected to occasional immersion in rainwater puddles or in freshwater from shoreborne seepage. Such brackish water can cause mantle oedema with anomalous nacreo-deposition. This is suspected to be the cause of the long and the short forms of *Gafrarium divaricatum* (Gmel.) (Boshoff, 1967a:spec. No. 94). Short forms are generally collected in the upper reaches of the intertidal zone while the long forms are predominantly subtidal in habitat. The abbreviated forms of *G. divaricatum* are usually covered by sand, thereby eliminating the possibility of a desiccating effect. The majority of examples of the forma *brevis* show normal growth up to the early adult region. Thereafter they acquire a series of compacted concentrics over the posterior region. These create a decrescendo of the posteriad expansion and at the same time augment the valve's convexity. Owing to unpredictable salinity variations, estuarine shells show an unusually large number of concentric cessation lines unless the individual mollusc is sited so favourably that the local salinity undulations are of a more subdued range.

The nature of attachment to the substratum and aggregation of specimens affect their shape, as seen in *Cardita*, *Isognomon*, *Malleus*, *Ostrea* and *Anomia* ("polymorphism" or paramorphism). Similarly, the chemical pigmentary changes under conditions of hypoxia

(*Ostrea* under sand) originate from the habitat (Korringa, 1956). When mud-living shells, such as *Lutraria inhacaensis* Boshoff, have excess of organic material in the habitat, they exhibit surface scars from acid etching and calcium absorption due to chemical substances produced by rotting material of the environment (Pl. IV, fig. 1). Lacustrine and fluviatile genera such as *Cafferia* and *Aspatharia*, are defaced by similar influences (Pl. V, figs. 1, 4.).

(*h*) **Invasive agents** may be of many kinds and merit a separate study. The environment where predisposition for such invasion is created, exists during marine pollution by sewage or factory effluent. Invasion by boring worms, sponges, algae and Bryozoa alter the shell characteristics of, e.g. *Perna perna* (Linn.), *Septifer bilocularis* (Linn.), *Chama gryphoides* Linn. and *Spondylus hystrix* Röding. In the presence of reduced resistance and decadency of habitat, borers like *Lithophaga*, *Petricola*, *Gastrochaena* and *Parapholas* seem to thrive on the larger molluscs (Boshoff, 1967b). It is suspected that in such a denuded, decadent or polluted area these borers are perhaps more easily discovered by a searcher and that the "increased borer population" is a false observation.

(*i*) **Traumatic agency.** The term is here restricted to physical trauma or fracture as a result of human activity or other sources of impaction (Pl. VI, figs. 1, 2.). Depending on the extent and penetrative involvement, the animal proceeds to attempt a repair or it succumbs.

The above list of ecological disturbances and processes which affect a bivalve may be modified or discarded if and when further research is conducted in this field of science. Strangely enough, the physio-pathological phenomena which so profoundly influence taxonomic criteria, have hitherto largely escaped attention. Paucity of literature on disease and the neglect of conchological pathology have assisted many a sick specimen to species status. These remarks on South African lamellibranchs therefore outline a field of study yet to be made and they stress the importance of observations relative to normal and abnormal ecological conditions during the collection and classification of marine specimens.

ACKNOWLEDGEMENTS

In alphabetical order, I wish to thank Prof. J. H. Day, Drs. N. Patterson, F. Spilkin, and Prof. C. Wyndham, for criticism and help.

REFERENCES

BARNARD, K. H., 1964. Contributions to the knowledge of S. Afr. marine mollusca, Part V, Lamellibranchiata. *Ann. S. Afr. Mus.*, **47**: 361-593.

BOSHOFF, P. H., 1967*a*. Pelecypoda of Inhaca Island, Mocambique. *Mems. Inst. Invest. cient. Mocamb.*, **7** (A): 65-206, 1965.

————1967*b*. Besoedeling van die see. *Tegnikon*, **15**: 189-193.

————1968. A note on some new Pelecypoda dredged off the Natal coast. *Trans. Roy. Soc. S. Afr.* (in press)

BOSHOFF, P. H. and FIELD, J., 1968. Pelecypoda dredged off the Natal coast. *Ibid.*

COOKE, A. H., 1959. Mollusca. In *The Cambridge Natural History*, **3**: 1-444, Codicote: Wheldon and Wesley.

FISCHER, P. H., 1950. *Vie et Moeurs des Mollusques*, pp. 253-262. Paris: *Payot.*

IREDALE, T., 1939. Mollusca, Part 1. *Scient. Rep. Gt. Barr. Reef Exped.* (1828-29) **5** (vi): 209-425, Ref. on pp. 268, 292.

KORRINGA, P., 1956. Oyster culture in South Africa (suppl. to Commerce and Industry (Mss. 1954), *Div. of Fisheries Invest. Rep.* **20**: 288-368. Ref. on p. 319.

TRYON, G. W., 1882. *Structural and Systematic Conchology*, **1**: 1-444, Philadelphia: Author's publication.

Date received: 12 November 1967